Labile Protogynous Hermaphroditism in the Black Bream, *Acanthopagrus butcheri* (Munro) (Sparidae)

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Black bream, Acanthopagrus butcheri, were sampled from three coastal lakes in south-eastern Australia. Of 19 specimens from the smallest, Hoyers Lake, seven had an ovotestis. Histological examination revealed that the ovarian part of each ovotestis was non-functional, but that spermatogenesis was occurring in the testicular tissue. Bream with ovotestes were 257-290 mm (SL) while all smaller fish were female and all larger individuals were male. Three of the 38 bream sampled from Myall Lakes had an ovotestis and the sex ratio of male:transitional:female was 12:3:23. No ovotestes were found in 52 fish from the relatively large Gippsland Lakes, where the sex ratio was approximately 1:1. We suggest that factors such as the size of the lake, extreme environmental conditions and intense fishing pressure may have contributed to the expression of different sex ratios and forms of sexuality, including protogynous hermaphroditism, in the three populations of A. butcheri.

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Introduction

The occurrence of hermaphroditism and other types of intersexuality in fish has long been recognized (see Atz, 1964). The superorder Teleostei is unique in having functional sex reversal occurring as a natural phenomenon, and in many species of some families, hermaphroditism and sex reversal constitute the normal mode of reproduction (Chan and Yeung, 1983). Members of the family Sparidae cover the complete range of hermaphroditic function, protandry (the most common), protogyny and synchronous hermaphroditism (usually a transitory condition) as well as gonochorism (Reinboth, 1970; Smith, 1975; Buxton and Garratt, 1990). Sex control in fishes is governed by both genetic and environmental factors, and it is well established that the environment can exert, under certain circumstances, a significant effect on the sex ratio or can initiate a sex change (Chan and Yeung, 1983).

The black bream, Acanthopagrus butcheri (Munro) and the yellowfin bream, A. australis (Gunther) provide important commercial and recreational fisheries in southeastern Australia (Fig. 1). These species are known to hybridize under certain conditions in estuaries and lakes on the south coast of N.S.W. (Rowland, 1984). Pollock (1985) found that A. australis undergoes protandrous sex inversion. This paper is the first report of protogynous hermaphroditism in the endemic Australian sparid, A. butcheri.

MATERIALS AND METHODS

Black bream were sampled using gill and seine nets from Gippsland Lakes, Victoria (52; standard length (SL) 112-288 mm), Myall Lakes (38; SL, 192-310 mm) and Hoyers Lake, New South Wales (19; SL, 201-325 mm) (Fig. 1). The latter site was sampled on two occasions, May and June.

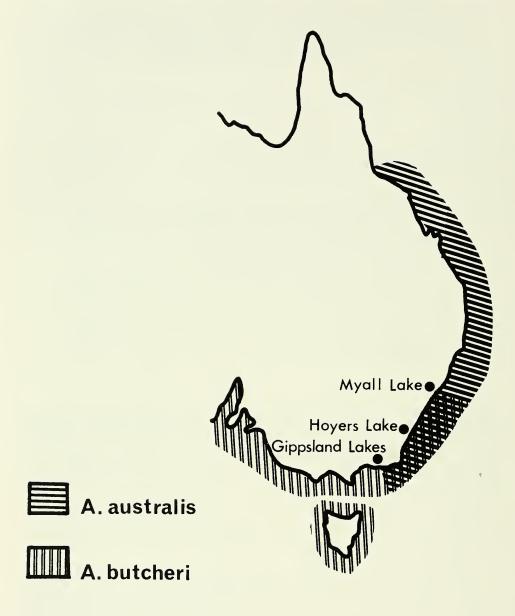


Fig. 1. Distribution of A. butcheri and A. australis in eastern Australia.

All gonads were examined macroscopically and their maturity determined according to the Hjort or International Maturity Scale (see Pollard, 1972). The gonads of all bream from Hoyers Lake and 10 (SL, 230-290 mm) from each of the other sites were preserved in Bodians fixative prior to histological examination. Sections, 7 um thick, were prepared from the middle of each gonadal lobe and stained in Harris' haematoxylin and eosin.

RESULTS

Of the 19 individuals taken from Hoyers Lake, four had a macroscopically visible ovotestis, and ovarian tissue was found in the testicular tissue of another three after histological examination. Three of the 38 bream from Myall Lake possessed an ovotestis, but none were found in the 52 specimens from the Gippsland Lakes.

Macroscopic Ovotestis Structure

The ovotestis in *A. butcheri* consisted of two lobes of approximately the same size. The ovarian tissue was situated medially on the dorsal surface of the testicular section and extended along its length. The ovarian tissue in an ovotestis was distinctly smaller than the ovaries in sex-separate females, but there was no distinct difference in the size of testes in ovotestes and sex-separate males of similar length. In two individuals, mature testes were convoluted and enveloped and obscured the ovarian tissue.

The ovarian parts of an ovotestis fused posteriorly, to form a common oviduct. The testicular parts did not unite, but connective tissue on the dorsal surface of each testis enveloped the fused ovaries, combining to give a single genital opening, posterior to the anus.

Ovotestis Histology

In transverse section, the ovarian tissue was always separated from the testis by a layer of connective tissue (Fig. 2). Amounts of ovarian tissue in each ovotestis varied. When there was a relatively large amount, the connective tissue layer surrounding the ovary was thick and usually contained clumps of spermatogenetic cells (Fig. 2a). In ovotestes where less ovarian tissue was present, it was usually embedded in a proliferation of connective tissue that formed a distinct lobe (Fig. 2b). Within several of these lobes, clumps of degenerate ovarian tissue enclosed by a layer of connective tissue were observed (Fig. 2c).

All bream sampled from Hoyers Lake in June were 'running-ripe' and contained sperm ducts and vas deferens extended with spermatozoa. The ovarian tissue in each ovotestis contained oocytes at several different maturation stages, but none were observed at or beyond the primary yolk stage (Fig. 3). In all oocytes that approached the primary yolk stage (and in many that reached the yolk vesicle stage) evidence of atresia was observed. Atretic oocytes were irregular in shape, the nucleus had moved from a central position, cytoplasmic detail was lost, the zona radiata had broken down and no yolk granules were present (Fig. 3b). The proportion of atretic oocytes appeared to be greater in a specimen captured in June compared to one captured in May.

Sex Ratio

The seven hermaphroditic bream from Hoyers Lake ranged from 265-290 mm (SL); smaller fish (with one exception) were all females, and those larger were all males (Table 1). In this sample of black bream there is a shift in the sex ratio with increasing length from all females to all males.

The bream sampled from Myall Lakes were mainly within the length range 200-299 mm and the sex ratio was skewed in favour of females; the ratio male: transitional:female being 12:3:23 (Table 2).

No ovotestes were observed macroscopically in the 52 bream from the Gippsland Lakes, and no ovotestes were identified in the 10 fish examined histologically. The ratio

of males to females in this population was 25:27, with both sexes being represented throughout the size range sampled (Table 2).



Fig. 2. Transverse sections (x3.1) of ovotestes in A. butcheri, sampled in: (a) May, 290 mm (SL); (b) June, 257 mm (SL); (c) June, 275 mm (SL).

Key to abbreviations: of - ovarian tissue; tf - testicular tissue; cf - connective tissue; sc - spermatogenetic cells.

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TABLE 1
Sex and sexual maturity of A. butcheri sampled from Hoyers Lake

Fish number	Month sampled (M — May) J — June)	Standard length (mm)	Sex and sexual maturity (macroscopically determined)	
			Female	Male
1	M	201	III*a	
2	M	210	IV^{*a}	
3	J	228	IV	
4	M	232	III	
5	M	240	IV	
6	J	253	IV	
7	M	257	III	IV
8	J	265	IV	
ý 9	Ĵ	275	IV^{*b}	V^{*a}
10	Ĵ	275	?	IV
11	M	280	?	V
12	M	285	5	V
13	M	285		V
14	M	290	III_{*p}	V
15	M	295		v
16	J	301		v
17	ĭ	303		īV
18	J M	305		V
19	J	325		V

^{**} III - developing; IV - maturing; V - mature.

TABLE 2
Sex ratio in three populations of A. butcheri

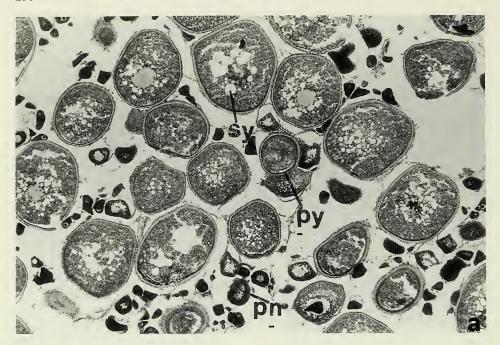
Range in standard length	Se	x ratio (male:transitional:	female)
(mm)	Hoyers Lake	Myall Lakes	Gippsland Lakes
150-199	_	_	2:0:3
200-249	0:0:6	5:0:12	10:0:10
250-299	1:7:1	5:3:11	9:0:11
300-349	4:0:0	2:0:0	4:0:3
Overall:			
150-349	5:7:7	12:3:23	25:0:27

DISCUSSION

Ovotestis Structure and Sex Ratio

The testicular part of an ovotestis in A. butcheri undergoes active spermatogenesis, and although oocyte development up to at least the yolk vesicle stage can occur, the ovarian part of the ovotestis is not fully functional. The predominance of atretic oocytes and the lack of yolky oocytes, the proliferation of connective tissue around the nonfunctional ovaries and the presence of degenerated ovarian tissue in the dorsal region of some ovotestes, suggest that these gonads were changing their functional role from female, through a transitory ovotestis in which only the testicular region was functional, to a sex-separate male. These observations, plus the shift in sex ratio from female to male with increase in body size, suggest that A. butcheri sampled from Hoyers Lake were protogynous hermaphrodites.

^{*}b, ovarian tissue contains many atretic oocytes.



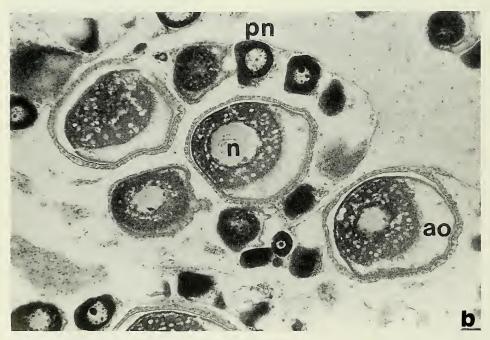


Fig. 3. Sections of ovarian tissue in A. butcheri: (a) ovary (x16) of sex-separate female, 253 mm (SL) May; (b) ovotestis (x53), 275 mm (SL): June.

Key to abbreviations: pn-perinucleolar oocyte; py-primary yolk oocyte; sy-secondary yolk oocyte; n-nucleus; ao-atretic oocyte.

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Influences on Gonad Development

The genetic mechanism for sex determination in bony fishes is primitive and labile (Dodd, 1960; Yamamoto, 1969) and although experimental studies of extrinsic factors on sex control and reversal are scanty because of technical difficulties (Chan and Yeung, 1983) it has been shown that environmental parameters can initiate a sex change in fishes. Harrington (1971) found that various combinations of day-length and temperature early in life, produced four sex phenotypes from one genotype of the cyprinodontid *Rivulus marmoratus*. Breder and Rosen (1966) suggested that hermaphroditism in *R. marmoratus* was an adaptation to the unstable coastal environment, and facilitated reproduction following severe population depletions caused by violent storms. Liem (1963, 1968) has shown that sex change in the protogynous rice field eel, *Monopterus albus* is related to the environment, and that the ability of some females to transform into males was of great importance in enabling each population to maintain full reproductive powers immediately after severe drought periods.

Hoyers Lake is a small (0.1 km²) shallow, coastal lake which although generally closed, periodically opens to the sea. The water in such lakes can undergo dramatic salinity changes (Scribner, 1985 pers. comm.). Since A. butcheri is considered to be confined to particular lake systems and seaward migration is limited (Butcher and Ling, 1962) recruitment to the local population from other estuaries is considered minimal. Because of the intense fishing pressure on fish over 254 mm total length (specific legal limit) the bream population in Hoyers Lake is at times dramatically reduced. Tomlinson (1966) and Ghiselin (1969) have shown that hermaphroditic species have an increasing advantage as populations become sparse. It is possible that the selective pressures produced by environmental conditions and/or intense fishing pressure have caused the expression of protogynous hermaphroditism in A. butcheri in this particular lake. A strategy of protogynous hermaphroditism would ensure that a large proportion of bream not taken by fishermen would be female. This would result in an increased zygotic production and maximisation of the next year class in comparison with a gonochoristic or protandrous form, under the same environmental conditions.

A. butcheri in Myall Lakes (101 km²) is subjected to pressure from both commercial and recreational fisheries. In addition fish kills involving bream occasionally occur in the lake (J. Bell, D. Dunstan, 1985 pers. comm.). These environmental factors may affect the expression of sexuality in this population. Although there was a decline in the bream fishery of the Gippsland Lakes (364 km²) between 1919 and 1943 (Butcher, 1945), A. butcheri in this relatively large lake system has probably not been subjected to the intensity of fishing pressure or extreme environmental changes which occur in the smaller Hoyers Lake. The lack of an ovotestis in 52 specimens and the approximate 1:1 sex ratio indicate that this population is gonochoristic.

The variation observed between these three populations of *A. butcheri* suggests that protogynous hermaphroditism is labile in this species. The complexity of sexuality among members of the family Sparidae is further demonstrated, and the results of this study demonstrate that environmental factors may be important in the determination of sex and sex ratios in sparids.

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